

Afforestation, restoration and regeneration — Not all trees are created equal

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Abstract: Undulations in weather patterns have caused climate shifts of increased frequency and duration around the world. The need for additional research and model data on this pressing problem has resulted in a plethora of research groups examining a particular tree species or biome for negative effects of climate change. This review aims to (1) collect and merge recent research data on regeneration within old- and new-growth forests, (2) highlight and expand upon selected topics for additional discussion, and (3) report how shade tolerance, drought tolerance, and inherent plasticity affect tree growth and development. Although shade and drought tolerance have been well studied by a number of research groups, this review reveals that in-depth analysis of a single or a few species in a given area will not generate the data required to implement a successful regeneration plan. Studies using historical accounts of previous species composition, information regarding site seasonality, species competition, and individual responses to drought and shade are needed to (1) develop best management plans and (2) ensure future modeling experiments are focused on a greater variety of species using more innovative methods to evaluate climate change effects.

Keywords: Climate change; shade tolerance; drought tolerance; canopy gaps; invasive species

Introduction

In an effort to preserve biodiversity, many countries were looking at reforestation and afforestation as important means of re-

plenishing the native flora and fauna. Haibara et al. (1989) described the differences between natural regeneration, survival of fallen seed, and artificial regeneration, and growth of seedlings planted as important distinctions to be made concerning reclamation of unused forest land, as planting of unsuitable species was non-beneficial. Afforestation of marginal land has relied primarily on native species with special emphasis on high value lumber species, such as oak and pecan being favored for both wood value and wildlife habitat. As the 21st century continues forests are likely to have dramatic shifts in composition and overall growth and development. Anthropogenic changes leading to decreased precipitation, increased temperatures, and extended drought are some of the most damaging conditions affecting reforestation efforts (Holmgren et al. 2012; Pawson et al. 2013). A lack of precipitation and belowground water resources leads to increased seedling mortality and extensive dieback in many species (Valdadares and Niinemets 2008; Hoffman et al. 2011), while others are minimally affected (Klopčič and Bocina 2012).

Forest conservationists and researchers seek to explore the available options for reforestation efforts while using collected climate data to attempt to anticipate future forest changes within a number of biomes. When considering the effects of anthropogenic changes on the landscape it is important to consider the ramifications of the demise of a single population. Forest composition is a collection of species working together in a highly balanced relationship. Extenuating circumstances such as altered precipitation regimes also have the ability to forever alter composition and future survival of a particular species within a forest niche (Gimmi et al. 2010). Vieilledent et al. (2010) modeled weeping silver fir (*Abies alba* ‘Pendula’) and Norway spruce (*Picea abies*) communities to determine if a mechanism for co-existence could be used to describe the competition relationship between the two species. The data showed higher mortality rates for Norway spruce than weeping silver fir in both larger and smaller saplings and lends credence to the idea of a “trade-off” theory within the niche examined. Recent work by Tanentzap et al. (2013) showed how a model built to examine *Betula* spp. responses to herbivory pressure can also be used to extrapolate and test forest management practices best suited for conservation

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scenarios.

Relationships between primary and secondary successional species are finely balanced so that each species is able to take advantage of momentary gaps in the canopy. Increased demand for wood products often spur growers into culling or clear-cutting forests at an accelerated rate (Hayes et al. 2005), thereby disrupting primary and secondary species interactions. The proper care and management of forestry plantations is essential for a continued regenerative effort if restoration of native forest cover is the final objective (Oliet and Jacobs 2012; Tullus et al. 2013) or if a healthy mixed-wood forest at multiple successional stages is desired (Cowell et al. 2010; Gaudio et al. 2011). As climates change a greater importance is placed upon modeling data to help ascertain where the future ranges of tree species will be located. With newly acquired modeling data researchers are able to adapt reforestation efforts to take advantage of new lands previously unsuitable for planting (Muñiz-Castro et al. 2011; Segarra Berenguer 2013). Sauer et al. (2012) noted that reforestation of marginal lands in four locations planted with either white pine (*Pinus strobus*), black walnut (*Juglans nigra*), and native hardwoods (*Quercus* spp., *Carya* spp., and *Acer* spp.), northern red oak (*Q. rubra*) and *Fraxinus* spp., white oak (*Q. alba* L.) and shagbark hickory (*Carya ovata* [Mill.] Koch), or white pine and Scots pine (*P. sylvestris*) led to improved soil organic carbon (SOC) content and an overall improvement in the land quality. Wang et al. (2013) noted that established exotic species such as *Acaia auriculaeformis*, and *A. mangium* required less soil N and maintained a greater proportion of N in above-ground biomass compared to native Chinese species such as *Castanopsis fissa*, *Schima superba*, *C. hystrix*, *Michelia macclurei* and two *Eucalyptus* spp. (*Eucalyptus urophylla*, *E. tereticornis*). A single native species *C. fissa*, was able to exhibit the same accelerated growth rate as exotics. Vlachodimos et al. (2013) showed that use of black locust (*Robinia pseudoacacia*) in reforestation and reclamation efforts of former mining areas dramatically improved soil organic mineral (carbon, nitrogen) and microbial biomass levels within two years. Black locust was also shown to be highly sensitive to stress thus it was recommended for removed after two years to allow for the planting of the native and less sensitive Italian oak (*Q. frainetto*) (Vlachodimos et al. 2013). Comparisons of native and exotic species traits are vital to increase the likelihood of forest recovery in degraded areas (Wang et al. 2013). Afforestation and reforestation efforts are important however, extensive research detailing current forest populations, growth rates, symbiotic associations, existing plant communities, and overall site characteristics are necessary if conservation and reforestation goals are to be attained in both tropical and temperate climates (Stanturf et al. 2004; Berkowitz 2013; Álvarez-Álvarez et al. 2013; Marín-Spiotta and Sharma 2013; Wang et al. 2013).

Use of modeling data as the basis for reforestation or afforestation efforts has predicted many anthropogenic-induced changes for a number of individual forest tree species. The phenotypic plasticity of a species is paramount to its survival (Fernandez et al. 2011). Plants endure unfavorable conditions using distinct adaptation mechanisms that are both species and region

specific. This work examined the variability in shade and drought tolerance among multiple tree species (Table 1). It synthesizes current research regarding the responses of forested stands to undulations in climate and speculates about the future composition of current forests. Recent data indicated that ensuring future survival of tree seedlings in a multitude of forest types is dependent upon the responses of various plant functional traits (Way and Oren 2010; Markesteijn et al. 2011a, b; Coursolle et al. 2012) therefore a few traits were selected for more in-depth study.

Influences on the regenerative effort

Seedling mortality

Climate change affects a number of variables in plant growth and development. Several of the primary effects were seen in seedling mortality rates. Fluctuations in soil moisture content, light, or temperature influence seedling growth and development as forested ecosystems contribute to global hydrologic cycles. Seedling mortality and survival, especially when planted on public lands, was typically influenced by a number of factors including drought, poor planting practices or herbicide drift from nearby lands therefore research must be conducted to ensure that any seedlings planted were able to endure the regions where they were expected to grow (Stanturf et al. 1998, 2004). Casperson and Kobe (2001) stated that seedling mortality in oak (*Quercus* spp.) and mixed hardwood forests during mesic conditions stayed low with increased growth among shade tolerant species however drought tolerant species such as northern red oak showed no variability when exposed to xeric conditions. Gómez-Aparicio et al. (2008) reported survival rates among four other genotypes of oak seedlings, Holm oak (*Q. ilex*), Pyrenean oak (*Q. pyrenaica*), cork oak (*Q. suber*), and Algerian oak (*Q. canariensis*) along resource gradients were dependent upon site specificity and resource availability. Data after two years predicted greater survival of Holm oak (58%) over Pyrenean oak (36%) at the drier site while Algerian oak (28%) outperformed Pyrenean oak (14%) and cork oak (11%) at the wetter site without irrigation. Resource conservation was the largest contributing factor influencing seedling survival. Variations in rainfall patterns expected to occur in the future would be detrimental to drought-sensitive species, primarily those native to temperate and boreal forest ranges. Reforestation studies have been conducted within boreal mixedwoods primarily composed of paper birch (*Betula papyrifera* Marsh.), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and black spruce (*P. mariana* Mill.). These studies demonstrated that black spruce seedlings had greater initial growth rates while lagging white spruce growth was attributed to increased sensitivity to abiotic stress. Despite showing slightly retarded initial growth white spruce could be successfully planted as a primary site species following clearcutting using enrichment (Thiffault et al. 2013).

Efforts to improve forest cover on open lichen woodlands by planting containerized black spruce in boreal regions have also

shown promise (Tremblay et al. 2013). With disk scarification and other site preparation methods, black and white spruce afforestation and reforestation attempts resulted in >90% survival although greater understanding of differential growth between stand types is needed before conclusions can be made (Thiffault et al. 2013; Tremblay et al. 2013). Steele et al. (2013) stated that seedling type was the primary factor influencing survival in Missouri Ozark restoration efforts with six *Quercus* spp. (bur oak (*Q. macrocarpa* Michx.), Northern red oak (*Q. rubra* L.), pin oak (*Q. palustris* Muenchh.), Shumard oak (*Q. shumardii* Buckl.), swamp white oak (*Q. bicolor* Willd.), and white oak (*Q. alba* L.)), two *Fraxinus* spp. (green ash (*F. pennsylvanica* Marsh.), white ash (*F. americana* L.)), pecan (*Carya illinoensis* (Wangenh.) K. Koch), black walnut (*Juglans nigra* L.), American sycamore (*Platanus occidentalis* L.), Eastern cottonwood (*Populus deltoides* Batr. ex Marsh.), and hackberry (*Celtis occidentalis* L.). Survival rates were higher in the ash species while height and growth rates were higher in sycamore, cottonwood and the ash species rather than oak species after two years. Depending on species, seedlings have varied effects on the microclimate of understory population and variable responses to site conditions. In European mountain ash (*Sorbus aucuparia*) sprouting increased the lifespan of understory individuals and decreased mortality rates (Zyweic and Holeksa 2012). American beech (*Fagus grandifolia* Ehrh.), black cherry (*Prunus serotina* L.), and yellow poplar (*Liriodendron tulipifera* L.) were each shown to affect microclimates differently because of varied transpiration rates and shade preferences (Siegert and Levia 2011). These works emphasized the fine balance achieved in the forest understory and highlight characteristics some species use to survive.

Seedling protection methods

Additional steps have been taken by research foresters to help protect newly planted seedlings. Potter and Hargrove (2012) used modeling data to develop 30,000 predicted ecoregions. These data will help lower seedling mortality rates by ensuring seeds planted in a particular region are suited to the future anticipated climate in an attempt to decrease seedling mortality because of regional incompatibility. Other researchers have used tree shelters which enhanced performance of American sycamore (*Platanus occidentalis*), green ash (*Fraxinus pennsylvanica* var. *subintegerrima*), and pin oak (*Q. palustris*) seedlings (Andrews et al. 2010) by regulating light levels or planting cover crops such as redtop grass (*Agrostis gigantea* Roth) and interplanting pioneer and seral species together (Dey et al. 2010, Steele et al. 2013) to decrease seedling mortality rates. Stanturf et al. (2004) and Mechergui et al. (2013) stated that tree shelters were essential for seedling survival in areas under herbivory pressure. Unfortunately, use of tree shelters can also lead to thin stems and inadequate root systems over time (Mechergui et al. 2013). A number of methods have been used to help increase seedling survival rates. Choice of method depends primarily on individual taste and the characteristics of the seedling planting site.

The moisture gradient

An important consideration for foresters attempting to replant seedlings or to initiate efforts to create a forested habitat is the soil type and its moisture retention ability (Table 1).

Table 1. An illustration of relative characteristics such as permeability, texture and water holding capacity for a variety of soils

Permeability class	Infiltration Rate (cm/hour)		
Very rapid	Greater than 25.4		
Rapid	12.7 to 25.4		
Moderately rapid	6.4 to 12.7		
Moderately rapid	2.0 to 6.4		
Moderately slow	0.5 to 2.0		
Slow	0.13 to 0.5		
Very slow	Less than 0.13		
Soil Texture	Water Capacity (cm water/m of soil)		
Coarse sand	2.1–3.6		
Fine sand	3.6–8.3		
Loamy sand	9.2–10		
Sandy loam	10.4–11.7		
Fine sandy loam	12.5–16.7		
Silt loam	16.7–20.8		
Silty clay loam	15–16.7		
Silty clay	12.5–14.2		
Clay	9.99–12.5		
Caveat	cm of water/m of soil		
	Sand	Loam	Silty clay loam
Saturation	43.3	48.4	50.8
Field capacity	17.5	31.7	36.7
Permanent wilting point	9.17	15	21.7
Oven dry	0	0	0
Gravitational	25.8	16.7	14.2
Water holding capacity	8.33	16.7	15
Plant available	4.17	8.33	7.5
Unavailable	9.17	15	21.7

Plant and Soil Sciences Library; Soils - Part 2: Physical Properties of Soil and Soil Water; 2011. Available at: <http://passel.unl.edu/pages/informationmodule.php?idinformationmodule=1130447039&topicorder=10&maxto=10>

As soil types often change within an area, analysis of soil type within an area could help decrease seedling losses due to drought. Planting schemea that seek to recharge soil water and account for canopy interception in seedling mortality was consistent along a soil moisture gradient and interpreted a weakly inverse relationship between shade tolerance and mortality during xeric conditions, an indication of drought tolerance (Casperson and Kobe 2001). In a study of habitat specialization with willow (*Salix* spp.), Savage and Cavendar-Bares (2012) noted “phylogenetic clustering” events occurred among species positioned along moisture gradients based upon drought tolerance capabilities. Research by Poulos et al. (2012) supported this work with a study of four pine (*Pinus* spp.) species including knobcone pine (*P. attenuata* Lem.), lodgepole pine (*P. contorta* Doug.), Coulter

pine (*P. coulteri* Don.), and sugar cone pine (*P. lambertiana* Doug.) that indicated the primary factors influencing distribution and mortality of these species was access to water and solar radiation resources. Despite being found in overlapping regions, variability in physiological responses was important in differentiating potential climate change responses within these species. Athy and Keiffer (2003) examined the effects of mulch on edaphic conditions and seedling survival on a vacated landfill. Restoration efforts on parcels such as landfills were urgently needed. Evaluation of mulch type and depth with respect to seedling survival rates of five different tree species (green ash, black locust, black cherry, bur oak (*Quercus macrocarpa*), and *Populus* spp.) were studied. Green ash exhibited the greatest survival with 97% of bareroot seedlings, while black cherry, black locust, and poplar benefitted from addition of mulch. Mechergui et al. (2013) evaluated mulch addition to cork oak seedlings and noted that mulching combined with tree shelters was required to improve seedling growth. Barajas-Guzman and Barradas (2013) showed increased survival rates of deciduous tropical forest species using alfalfa straw, bare soil, forest litter, and white polyethylene mulches. Polyethylene mulch boasted the greatest survival rates and the lowest cost. These findings indicated that regeneration and reforestation efforts on other sites may benefit from mulch addition.

Tree morphology

A number of morphological traits are considered essential for survival during unfavorable conditions. Mund et al. (2010) studied an old-growth forest composed primarily of European beech (*Fagus sylvatica*), with European ash (*Fraxinus excelsior*) and sycamore (*Acer pseudoplatanus*) making up most of the remainder of the tree species present, to determine if a connection could be found between weather and stem growth of the three species. European beech stem growth was accelerated after a warm spring while stem growth in European ash was improved following above-average precipitation levels in June. Mund et al. (2010) noted that stem growth began after a week of consecutive 10 °C (Menzel 2003; Menzel et al. 2006; Mund et al. 2010) temperatures. Application of this methodology to European ash was accurate, while European beech and sycamore did not respond for greater than 90 days perhaps indicating that responses to increased temperatures were likely species specific. Young plantings of European ash were determined to perform better when pre-selected based upon shoot and root morphologies. Superior seedlings were 40–50 cm tall with numerous fine roots in a fasciculate system (Maltoni et al. 2010) while later studies of cherrybark oak (*Q. pagoda* Raf.), green ash, Nuttall oak (*Q. nuttallii* Palmer), sweet pecan (*Carya illinoensis* (Wangenh.) K. Koch), and water oak (*Q. nigra* L.) used additional morphological traits such as root volume, fresh mass, and number of first order lateral roots to determine which seedlings should be outplanted for maximal survival (Jacobs et al. 2012). Additional relationships were also found between coarse and fine roots in *Shorea* spp., *Dipterocarpus* spp., and *Leguminosae* spp. (Kosugi

et al. 2009; Makita et al. 2012). Mataruga et al. (2012) used studies of Austrian pine (*P. nigra* Arnold) to determine higher seed quality rather than provenance was of the utmost importance for improving survival rates under drought conditions. Leites et al. (2012) also noted the limitations of provenance tests for inferring anthropogenic-induced growth responses in western larch (*Larix occidentalis* Nutt.). These studies indicated multiple morphological traits improve species survival.

Tolerance levels and survival

Selection of trees for afforestation or reforestation is a process requiring a thorough understanding of an individual species and its abiotic and biotic stress tolerances (Vyse et al. 2013). Numerous papers discuss the importance of drought tolerance or shade tolerance and how higher levels of either or both characteristics are essential for the survival of many tree species (Appendix 1). Sack et al. (2003) indicated that tolerance to both shade and drought in a mixed oak forest, whether achieved via functional morphology or by other means, may prove to be invaluable as droughts become more frequent worldwide. Sack (2004) predicted species with tolerance to both shade and drought would quickly become the primary species in understory populations in forests as climates become drier. These data have encouraged a shift from growing less tolerant species to more tolerant ones however, Hanberry et al. (2012) suggested that planting sweetgum (*Liquidambar styraciflua*) and oak species were more advantageous than planting ash because shade-tolerant ash would change current species interactions rather than pursue restoration of compatible native tree species. Tree species accustomed to an understory climate may be better prepared to deal with the extreme shifts in weather patterns predicted to occur but could alter the existing forest dynamic. Work by Siegert and Levina (2011) showed that understory American beech and black cherry had significantly lower water loss than an understory of black cherry and yellow poplar without shade and postulated that understory seedlings were better able to utilize water resources during drought periods. Determination of seedling mortality using shade tolerance levels has been reported in a number of works (Kobe et al. 1995; Bloor and Grubb 2003; Metslaid et al. 2007; Takahashi 2010). Additional research has indicated that increased seedling diameter and shade tolerance correlated to increased mortality as opposed to decreased shade tolerance levels (Mason et al. 2004). Kunstler et al. (2009) and Rueger et al. (2011a) reported that shade tolerance decreased mortality however an additional trait to consider was tree diameter, reported to be most influential in survival. Those trees studied with larger diameters were less susceptible to death although limits to this effect were seen. In Coigüe de Chiloé (*Northofagus nitida* [Phil.] Krasser) studies, increased light significantly increased tree height (Coopman et al. 2011) while studies of crown lengths in Rocky Mountain fir (*Abies lasiocarpa* [Hook] Nutt.) and Engelmann spruce (*Picea engelmannii* [Parry] Engelm.) showed no significant difference except when responding to increased competition from neighbors (Antos et al. 2010).

Canopy gaps

The introduction of a break or “gap” in the forest canopy encourages a flurry of growth as shade-intolerant species, and species with root suckers quickly colonize the newly available space. Reforestation attempts that fail to recognize the value or influence of gaps within the canopy may not be as well thought out as others. Rodriguez-Calcerrada et al. (2010) noted that removal of canopy cover can improve seedling regeneration however Rodriguez-Calcerrada et al. (2011) noted that selective thinning of Holm oak where throughfall was reduced did not influence stem growth but did decrease viable acorn numbers. Removal of unhealthy stems was proposed to help remaining stems withstand drought increase viable acorn production. Growth of bitter cherry (*Prunus emarginata*) in the understory of Douglas fir (*Pseudotsuga menziesii*) forests required gaps or complete canopy removal as greater than 80% of seedlings were found in gap areas (Brown and Antos 2012). In a study of tropical pioneer species, it was determined that canopy gap size determined which species would colonize the area first. Goodale et al. (2012) reported that the high light species *Trema* (*Trema orientalis*) and *Osyris peltata* (*Macaranga peltata*) colonized large gaps while *Uppila* (*Macaranga indica*), *Dillenia triquetra*, *Kekiri-wara* (*Schumacheria castaneifolia*), and *Wendlandia bicuspidata* preferred smaller gaps. Two other species, *Batino* (*Alstonia macrophylla*) and Indian rhododendron (*Melastoma malabathricum*), were found in a variation of gap sizes in accordance with a wider range of light and shade tolerances. Use of canopy gaps to anticipate species compartmentalization is not an exact science. A recent study with koa (*Acacia koa*) showed natural regeneration by root suckering occurred without a canopy gap although the majority of suckers extended along and beyond forest edges (Scowcroft and Yeh 2013). Coexistence of shade-tolerant and intolerant species within gaps has been seen between European beech, silver fir (*Abies alba*), and sycamore although sycamore, a very shade-intolerant tree, only reached full height within large gaps (Nagel et al. 2010). Caquet et al. (2010) noted coexisting European beech, sycamore, field maple (*Acer campestre*), and Norway maple (*Acer platanoides*) all responded positively to gap openings although Norway maple and sycamore achieved greater tree heights. In a study of three stands of composed of California boxelder (*Acer negundo*), willow, aspen, and ash at varied disturbance levels, Saccone et al. (2010a, b) noted California boxelder demonstrated higher growth in gaps than native ash and exhibited growth comparable to the fast-growing aspen and willow species under both high and low light conditions.

Gap size and species composition

Gap size also influences species composition and effects should be understood before reforestation efforts begin. To determine if gap size would be effective in anticipation of tree biomass and future composition Dyer et al. (2010) created large, medium, and small gaps within a forest composed of a sugar maple (*Acer saccharum* Marsh.) dominated overstory although white ash

(*Fraxinus americana* L.), basswood (*Tilia americana* L.), and bitternut hickory (*Carya cordiformis* [Wangenh.] Koch) were also present. Sugar maple also dominated the understory and seedling layer with seedlings of white ash, bitternut hickory, and ironwood (*Ostrya virginiana* [Mill.] Koch) also at high densities within the sapling layer. Gasser et al. (2010) noted gaps of variable sizes could promote regeneration of both sugar maple and yellow birch (*Betula alleghaniensis* Britton). Greater growth was obtained as gap sizes increased however, competition from understory vegetation within large gaps hindered growth of yellow birch more than sugar maple. A recent study of Aleppo pine (*Pinus halepensis*) suggested that thinning increased total litter-fall, decreased competition stress, and heightened vigor leading to greater total biomass (Navarro et al. 2013). A consensus among these research findings indicated that gaps of various sizes could prove beneficial for species regeneration.

Gap edge effects and forest regeneration

The forest regenerative effort involves more than growth within canopy gaps as these openings are quickly closed when new seedlings emerge. Canopy gaps are vital for many species. Dyer et al. (2010) noted the greatest growth and productivity occurred along forest edges rather than within gaps. In a forest dominated by Japanese blue oak (*Quercus glauca*), Japanese privet (*Ligustrum japonicum*), and Japanese cheesewood (*Pittosporum tobira*) shorter heights were seen in Japanese blue oak and Japanese privet growing in the interior and greater stem numbers were seen on the edge (Yoko-o et al. 2011). Wicklein et al. (2012) noted that these “edge effects” became less pronounced as the edge trees matured and suggested that response to light was paramount to determining forest species density and composition along gap edges. Suzuki et al. (2012) noted edge influences in small (< 2 ha) fragmented forest areas could extend to cover the expanse entirely and work to influence future population densities. Incorporation of variation in canopy gaps and crown sizes was proposed to positively influence mountain pine and silver fir forest dynamics however Scots pine forests were negatively affected (Ameztegui et al. 2012). Prevosto et al. (2011) noted in that use of burning and scarification encouraged rapid growth of shade-intolerant species however this influx was short-lived as the shade-intolerant Aleppo pine slowly crowded out opportunistic gap species.

Gaps and forest progression

During progression of a forest from primary to secondary stages, most shade-intolerant species numbers declined as the canopies closed and densities of shade-tolerant trees increased. In a temperate tropical forest, presence of tropical or shade tolerant species in the canopy was rare despite having higher densities of tropical species to temperate tree species (Muniz-Castro et al. 2012). Sarr et al. (2011) noted regeneration of a majority of species was greater in gaps. Formation of canopy gaps by one species may be beneficial to other species such as the relationship seen between broadleaf podocarpus (*Podocarpus nagi*) and green

bolly gum (*Neolitsea aciculata*) (Nanami et al. 2011). Beaudet et al. 2011 used the SORTIE-ND model on boreal mixedwood stands to determine how introduction of canopy gaps affected growth of understory species. The authors attempted to predict future stand productivity with selection harvest of overstory species and noted a uniform harvest pattern allowed greater volumes to be removed without disrupting light levels preferred by shade intolerant species. Van Do et al. (2011) noted that *Wendlandia paniculata*, needlewood (*Schima wallichii*), tsaii (*Camellia tsaii*), and dedo (*Lithocarpus ducampii*) were able to positively influence species recruitment during primary forest initiation and after several decades diversity had tripled. These findings lead credence to findings of Queenborough et al. (2007) with several evergreen trees in the Myristicaceae family. Promis et al. (2010a, b) reported similar findings as Magellan's beech (*Northofagus betuloides*) seedlings and saplings are relatively shade tolerant and continuously regenerate to develop a multi-aged forest structure. It was also proposed that this shelterwood system could be sustainably managed while maintaining biodiversity. Wang et al. (2010) looked at the correlation between shade-tolerance and life expectancy for a number of trees of different sizes, ages, and tolerances during a forest inventory analysis and noted species compositions were likely to revert to primary forest configurations over time. A thorough review of the interaction between shade and drought conditions was written by Holmgren et al. (2012).

Gaps and forest composition

Canopy gaps as a result of treefall are vital for the continued diversity of tree species within a forest (Bentos et al. 2013). Introduction of a gap within a closed canopy also spurs accelerated growth in shade-intolerant species. These species quickly partition carbon into aboveground biomass (AGB) to increase both height and diameter. Analyses that focus on tree height and diameter alone without considering the effect of light tend to overlook additional plasticities within each species type (Rueger et al. 2011b). Comparison between coniferous (Masson's pine (*Pinus massoniana*), slash pine (*Pinus elliottii*)), broad-leaved (Chinese sweetgum (*Liquidamber formosana*), schima (*Schima superba*)), and mixed-species forests in China however, failed to show significant differences between above- and below-ground biomass although soil organic carbon (SOC) within coniferous forests was up to 25% less (Wei et al. 2013). A number of additional traits are important when attempting to predict future forest composition such as seed size and weight (Takahashi 2010; Hill et al. 2012; Wahid and Bounoua 2013), wood density (Joseph-Wright et al. 2010), soil characteristics (Rueger et al. 2011b), topography (Bentos et al. 2013), and herbivory (Rueger et al. 2011b). Kabzems et al. (2011) compared quaking aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* [Moench] Voss.) responses to light and noted increased diameter in spruce rather than height. In a forest dominated by shade-tolerant tawa (*Beilschmiedia tawa*), Carswell et al. (2012) studied the light responses of the two conifer species miro (*Prumnopitys ferruginea*) and rimu (*Dacrydium cupressinum*). Rimu, typically a

shade-intolerant species, attained the greatest height and stem diameter. Both conifer species were able to grow under a number of light conditions. These data indicated that the forest would likely shift in dominance from tawa to miro and rimu species. Distribution of Oriental beech (*Fagus orientalis* Lipsky) seedlings was found to be size-related with smaller trees being found clustered together during each growth stage (Akhaven et al. 2012). Jarcuska and Barna (2011a) looked at a variation of light conditions on the growth response of European beech when compared to results of Caquet et al. (2010). The lag in growth responses of European beech seedlings in the Jarcuska and Barna (2011b) study was attributed to the larger scope of light conditions examined. Additional research into canopy gaps and size-density relationships in beech was suggested to resolve the issue.

The presence of numerous stems of similar size within a forest indicates the presence of early species competition. Boivin et al. (2010) noted dense stands of size and age-matched stems in a boreal mixedwood forest. Interestingly, the most dominant competitor was balsam fir rather than the aggressive quaking aspen, a fast-growing opportunistic species. Typically aspen is highly competitive within forests and can quickly colonize and dominate both gap and canopy areas. Species with weak competitive abilities, such as English yew (*Taxus baccata*), are less likely to be widely distributed and more likely to exist within smaller niches without competition (Iszkulo et al. 2012). Ability to take advantage of canopy gaps is important for the continued success of wet forest species where gaps close quickly and understory light is limited (Brenes-Arguedas et al. 2011). Hitsuma et al. (2012) noted in a study of hiba (*Thujopsis dolabrata* 'Hondai') that despite the negative effect of photoinhibition hiba seedlings exhibited a more positive growth response to the increased light which countered the damage from photoinhibition. Rebbeck et al. (2012) reported in a study of three *Quercus* spp. northern red oak, chestnut oak (*Quercus prinus* L.), and white oak that the slowest growing species, white oak showed the greatest light-use efficiency (LUE). Csontos et al. (2001) noted that changing light conditions were directly related to the basal diameter of manna ash (*F. ornus*) trees. These data indicated undulations in light and abiotic influences, such as drought negatively influenced growth.

Invasives

As temperature rise and precipitation wanes trees species that were once prominent in an area are dying out. These native species are being replaced by more tolerant invasive species (Table 2). Reynolds and Cooper (2010) used data collected from a study of salt cedar (*Tamarix ramosissima*), Chinese hemlock (*Tsuga chinensis*), and cottonwood (*P. nigra*) hybrids to show how the invasive Russian olive (*Elaeagnus angustifolia*) can outperform native species in low light and moisture conditions. Morecroft et al. (2008) looked at rates of intrusion for sycamore in forests dominated by European ash and pedunculate oak (*Q. robur*), and noted that because of its slower growth rate than ash, its stunted growth during dry periods, and the fact that climate was predicted to become more dry, sycamore was unlikely to compete

with ash for habitat and would likely die out. The ability of most *Fraxinus* spp. to take over an unclaimed area reflects positively on its use in regeneration efforts but susceptibility to pests makes planting them a risk. Karnitz and Asbjornsen (2006) evaluated the composition, age, and structure of an oak savanna, and noted that over time the stand also supported green ash, shagbark hickory, American elm (*Ulmus americana* L.), and ironwood species. Age dating of the trees showed growth of non-oak species occurred in the aftermath of the cessation of grazing and cutting activity. Martin et al. (2010) compared survival characteristics of shade-intolerant tree-of-heaven (*Ailanthus altissima*) and shade-tolerant invasive Norway maple in a closed canopy forest using modeling. The accelerated growth of Norway maple in low light was compared to the increased mortality of tree-of-heaven to demonstrate how species densities can be altered by non-native species. This adaptive plasticity is likely found in other highly invasive species.

Table 2. List of some of the most prevalent invasive tree and grass species in the United States with growth region habitat included

Scientific Name	Designation	Region/Habitat Preference
<i>Arundo donax</i>	perennial grass	temperate, riparian areas
<i>Bromus inermis</i>	grass	temperate, grasslands
<i>Bromus rubens</i>	bunchgrass	cool areas, dry, shallow soil
<i>Cortaderia jubata</i>	tussock grass	coastal, grassland sites
<i>Miscanthus sinensis</i>	grass	no preference noted
<i>Nassella tenuissima</i>	grass	grasslands, grazing areas
<i>Phalaris arundinacea</i>	perennial grass	cool wet habitats
<i>Phragmites australis</i>	marsh grass	tidal and nontidal marshes
<i>Rottboellia cochinchinensis</i>	grass	subtropical climates
<i>Schismus barbatus</i>	grass	desert conditions
<i>Sorghum halepense</i>	grass	no preference noted
<i>Spartina anglica</i>	salt marsh grass	tidal marshes
<i>Acer ginnala</i>	tree	temperate zones
<i>Ailanthus altissima</i>	tree, shrub	riparian zones
<i>Albizia julibrissin</i>	tree	riparian zones
<i>Annona glabra</i>	tree	riparian zones, wetlands
<i>Cinnamomum camphora</i>	tree	coastal, grassland sites
<i>Citharexylum spinosum</i>	tree	tropical climates
<i>Dalbergia sissoo</i>	tree	tropical climates
<i>Elaeagnus angustifolia</i>	tree, shrub	floodplains, riverbanks, marshes
<i>Ficus rubiginosa</i>	tree, shrub	temperate zones
<i>Paulownia tomentosa</i>	tree	moist, well-drained areas
<i>Pinus</i> spp.	tree	temperate, riparian areas
<i>Populus</i> spp.	tree	moist, well-drained areas
<i>Prosopis</i> spp.	tree, shrub	temperate zones, desert conditions
<i>Psidium cattleianum</i>	tree, shrub	subtropical climates
<i>Rhizophora mangle</i>	tree, shrub, aquatic plant	swamps, riparian zones
<i>Rhodomyrtus tomentosa</i>	tree, shrub	subtropical climates
<i>Robinia pseudoacacia</i>	tree	dry savannas, grassland

Note: Data compiled from <http://plants.usda.gov/java/> and <http://www.issg.org/database/welcome/>

Removal of invasives in an attempt to restore native species has been attempted. Hartman and McCarthy (2004) reported on their attempts at forest restoration and native diversity in areas where invasive species such as Amur honeysuckle (*Lonicera maackii*) had been eradicated. Use of multiple site locations and increased growing space would allow for the differential survival of native species planted for rejuvenation of the area. Comparison of survival rates indicated green ash was the most adaptable followed by chinkapin oak (*Quercus muehlenbergii*), black cherry, and black walnut with similar survival rates, the lowest rates were those of Eastern redbud (*Cercis canadensis*) and flowering dogwood (*Cornus florida*). This differential survival had been noted in other studies where invasives had been removed and was attributed to individual species responses to microclimate (Sweeney et al. 2002). Grotkopp and Rejmánek (2007) proposed in a study which compared aggressive invasive species with less aggressive invasives that the highly invasive woody species were more likely to outcompete and dominate native or less-invasive woody species if these had optimal seedling growth rates, greater specific leaf area, and root allocation. These advantages allow highly invasive species to survive conditions that decimate other species.

Invasives and afforestation efforts

Although invasive species interfere with forest dynamics they can be used to repurpose marginal lands if kept in check. Khamzina et al. (2006) looked at the morphology and physiology of ten tree species apricot (*Prunus armeniaca* L.), black poplar, black willow (*Salix nigra* Marshall), Chinese cedar (*Biota orientalis* L.), Euphrates poplar (*Populus euphratica* Olivier), Russian olive, salt cedar (*Tamarix androssowii*), Siberian elm (*Ulmus pumila* L.), green ash, and white mulberry (*Morus alba* L.) to determine the suitability for afforestation of degraded landscapes with loam or sandy soils. Of the species examined, it was noted that Russian olive and Euphrates poplar were best suited for afforestation efforts when numerous growth characteristics were analyzed. The introduction of these species into fallow plantations may help to rejuvenate soils, however the authors encouraged a thorough understanding of the characteristics of trees considered for introduction to ensure suitability as both of these species can be classified as invasive. Gyenge et al. (2003) measured an increase in productivity of a Chilean cedar (*Austrocedrus chilensis*), forest as Ponderosa pine began to invade. In a follow-up study by Gyenge et al. (2008), annual productivity of the invasive ponderosa pine was twice that of the native Chilean cedar, and observed differences in hydraulic conductance were likely contributing factors as ponderosa pines had higher growth and transpiration rates than Chilean cedar. The authors also affirmed that Chilean cedars were limited in carbon fixation capabilities although additional research was needed to corroborate these data. Another study in pine, concerning afforestation, indicated that Aleppo pine populations most often found in the Mediterranean basin tended to deplete water reserves and alter $\delta^{13}\text{C}$ compositions when planted in semiarid regions. However, other studies indicated that Aleppo pine plantings improved soil fertil-

ity and microclimate (Maestre et al. 2003). Querejeta et al. (2008) indicated that addition of urban soil refuse may improve nutrient availability, WUE, and overall survival of the Aleppo pine seedlings. Unfortunately, the rapid growth of the trees in response to this treatment could not be supported by the available soil moisture causing forests to exhaust water supplies. The authors presented yet another example of why afforestation efforts must be closely monitored to ensure that the proposed location was capable of supporting newly planted tree species. Maestre and Cortina (2004) stated that afforestation efforts with Aleppo pine were responsible for decreased bird biodiversity and increased pest outbreaks. The authors suggested that afforestation efforts should be revised, as single-species plantations used to restore arid regions were ineffective because of the displaced native shrubs and fauna in that particular region. Efforts should be made to determine alternative solutions to afforestation in highly sensitive regions. Newsome et al. (2010) proposed that addition of western larch to non-timber stands could increase species diversity without ill effects. A review by Pausas et al. (2004) indicated that intermingling different species (e.g. broad-leaved species) into a pine forest or other restoration techniques, such as management of animal dispersal may be needed to benefit different expanses of the landscape. These methods will work to prevent biodiversity losses and to promote reforestation efforts.

Stand responses

Tree species that take longer to become established are most vulnerable to climate change. Hurst et al. (2012) noted smaller, slower growing trees were likely to have increased rates of mortality as were species such as red beech (*Northofagus fusca*) regenerating within disturbed stands. Frequency of disturbance may lead to long-term changes in forest composition. Understanding inherent physiological traits of a species is imperative to know before reforestation is attempted (Poulos et al. 2012). When grown in highly heterogeneous soil moisture and light habitats, basal diameter was no longer an accurate indicator of tree age while those trees grown in homogeneous high light and constant soil moisture areas were able to be aged using basal diameter. Comeau et al. (2010) focused on size-density relationships of Douglas fir and Sitka spruce (*Picea sitchensis* [Bong.] Carr.) and presented the maximum stem densities and sizes for use in stand management. Rathbun et al. (2010) used basal area of large trees, height, and DBH as indicators of predicted mortality within western hemlock and western red cedar stands based on logic model output data. These indicators resulted in poor approximations for smaller trees and accurate predictions for larger ones thus leading Rathbun et al. (2010) to conclude that a gap existed in modeling survival data across size classes. Luo and Chen (2011) reported that mortality of jack pine (*Pinus banksiana*), quaking aspen, paper birch, and black spruce was usually less aligned with size and more closely related to physiological traits. Size-density relationships among these species indicated that mortality increased in crowded stands although paper birch displayed greater rates of mortality in less crowded

conditions an indication that stem density plays a part in predicting future forest composition. In addition, Luo et al. (2012) reported that density dependence was less important than habitat beyond early growth stages. A recent study by Tanentzap et al. (2013) examined regeneration responses to afforestation efforts with *Betula* spp. grown in either small 0.1 ha patches or a 16 ha block. It was determined that the larger patch increased regeneration while the smaller patches encouraged stochasticity and later extinction based on simulation modeling. Use of Ecological-niche modeling (ENM) combined with GARP (Genetic Algorithm for Rule-Set Prediction) and MaxEnt (Maximum Entropy) models of cork oak populations uncovered data useful for determining populations in need of immediate restoration as opposed to those where the need was not as great. The obtained data were used to predict potential cork oak distribution over time and identify barriers to further geographic establishment (Vessella and Schirone 2013). Thus, modeling efforts are necessary to understand long-term results of conservation and restoration efforts for both flora and fauna.

Climate change and forest development

An important consideration for forest composition and development is climate change. Climate change was predicted to bring greater winter precipitation levels in conjunction with warmer, drier summers, which according to Mote et al. (2003), and West et al. (2007a, b), were likely to illicit detrimental effects in forests of all ages. Wharton et al. (2009) examined stand age effects on ecosystem mass and energy exchanges in response to seasonal drought in two early-growth and one old-growth Douglas fir forests. The authors indicated that because of predicted climate change scenarios in forests of the Pacific Northwest, younger forests had a more difficult time becoming established as old-growth forests tended to have roots able to reach water at greater depths than younger forests which had heightened sensitivities to water shortages. Thus, Wharton et al. (2009) suggested further studies involving additional successional stages to thoroughly address these problems. Because of limitations in the water available for each plant or tree in a given area, the primary factor affecting productivity (Long et al. 2004), the density at which vegetation was spaced was imperative to its ability to obtain a sufficient amount of water for optimal growth and development (Querejeta et al. 2008, Guo and Shao 2013). In addition to effects of stand age on survival during drought Coursolle et al. (2012) noted juvenile trees in afforested white pine stands as opposed to mature trees in black spruce, jack pine, aspen, Douglas fir and mixed-wood stands became carbon sinks for the first 4 years rather than sources for the first 10 to 20 years after planting. Low productivity within plantations can be also be attributed to location within northern regions. Recent studies of Willow (*Salix purpurea* L.) showed nutrient levels fluctuated after initial rotations and recovered more slowly depending on temperature and degree of soil disturbance (Ens et al. 2013). Charnley et al. (2010) provided a review of some of the methods small-scale farmers can use to maximize reforestation or afforestation efforts and the resulting carbon sequestration effects.

Predicting climate change effects

A review of climate change responses in trees was written by Way and Oren (2010) and although not species-specific, their modeling data determined tropical species more so than any other forest group (temperate, boreal), were most vulnerable to negative effects of climate change. The authors outlined the various equations that could be used to explain responses on a larger scale. Omeja et al. (2011) and Roman-Cuesta et al. (2011) stated that increased fire control measures would be beneficial in protecting remaining tropical forests while Wright (2010) reported that tropical forests have already demonstrated accelerated structural changes in response to climate change combined with deforestation during the pre-industrial age (Nevle et al. 2011) and before government protection strategies were initiated. However, van Breugel et al. (2011) concluded that modeling data used as the basis for management and reforestation efforts should be examined carefully as predictions of AGB undulated between allometric AGB models. Increased stem densities within forests may lead to decreased growth and development or self-thinning. Rivoire and Le Moguegec (2012) analyzed data obtained from self-thinning within European beech, sessile oak (*Quercus petraea* [Mattuschka] Liebl) and pedunculate oak, and Norway spruce mixed-forests to develop equations to determine the most cohesive stem density for forest tree species. It was surmised that the equation could also be used for other forest types provided enough data were available. It is important to have models to help with the prediction of future forest composition however Pantic et al. (2011) showed that silver fir would abstain from growth for long periods (between 40 and 330 years) termed “stagnation stages” because of limited growing space. Surprisingly, when growth is resumed, no negative developmental effects were seen. Continued competition between forest tree species makes it difficult to determine carbon storage capabilities (Woodall et al. 2011). Therefore, knowledge of previous forest composition is necessary to ascertain possible future growth and host range suitability (Sarr et al. 2011) and is also vital in the long-term for successful forest population establishment (Williams and Dumroese 2013). A review by Brockerhoff et al. (2013) regarding *Eucalyptus* plantations indicated that there is no one particular management plan that can be used in forest reforestation efforts because of both site- and tree-specific requirements. Additional growth stimulants such as supplemental organic material (i.e. nurse logs) are important considerations for reforestation efforts with species such as (*Tsuga heterophylla* (Raf.) Sarg.) and Sitka spruce (Pabst and Spies 1999, Sarr et al. 2011).

Forest growth and seasonal shifts

Understanding seasonal shifts within a site is imperative for reforestation efforts and those sites with highly variable conditions are often responsible for decreased performance in reforestation efforts. Craven et al. (2011) showed with *Terminalia amazonia*, *Inga punctata*, *Colubrina glandulosa*, *Tectona grandis*, *P. guachapele*, and *Acacia mangium* that overall adaptations to drought

are essential for survival on sites with fluctuating climates. Linderson et al. (2007) examined stand-level productivity within a willow plantation and noted both transpiration and WUE were influenced depending on evaluation method and hybrid. Willow clones were able to adjust to water shortages; however the ability of seedlings to utilize photosynthetically active radiation was compromised, resulting in decreased stem biomass in a subset of clones. The authors rationalized that this minimization in stem biomass could be a result of a change in nutrient allocation for growth. Although no indication was made as to where the enhanced growth may be, Linderson et al. (2007) indicated that perhaps more efforts were made to increase WUE thereby draining the nutrient pool. Livingston et al. (1995) reported on the canopy dieback of black ash (*F. nigra*) populations in Maine, and based on stream flow data determined that drought was the causative agent. Auclair et al. (2010) reaffirmed the results of Livingston et al. (1995) that indicated winter dieback was an indication of freezing injury to roots, a condition exacerbated during summer drought. They also presented data on the recent development of a model that predicted timing and dieback in sugar maple, white ash, green ash, black ash, *Betula* spp., red spruce (*Picea rubens* Sarg.), and Spanish black pine (*Pinus nigra* Am. ssp. *salzmannii*) (Lucas-Borja et al. 2011). Precipitation totals from Long-term Ecological Research (LTER) sites nationwide emphasized the shifts being described in the research community (Table 4).

Interactions affecting stand dynamics

The interactions among forest species are most often the driving force in determining stand composition and species survival. In a study of bottomland forest species Berkowitz (2013) stated that evaluations of both ground cover and shrub: sapling densities would be useful indicators of successful reforestation efforts. Le Goff et al. (2011) looked at shade tolerance, size-density, and mortality relationships between ash and beech and oak and sycamore. Shade tolerance among the different species did not appear to affect mortality rate. Puertolas et al. (2010) noted that root growth was negatively affected as light levels decreased in studies of shade intolerant Aleppo pine and comparison with Holm oak showed that the shade-tolerant Holm oak was unaffected during wet conditions. During the dry season mortality in Holm oak was lower than Aleppo pine because of its increased shade tolerance. Petritan et al. (2011) noted that conversion of Norway spruce stands into mixed stands dominated with European beech, Douglas fir, and several other species that increased root competition led to greater mortality in Douglas fir saplings rather than European beech. Light accelerated root growth and tree height when Douglas fir root competition was removed (Petritan et al. 2011). Conversion of a native forest to a Monterey pine (*Pinus radiata*) plantation forest resulted in decreased shading and species richness (Meers et al. 2010). Decreased diversity has also been seen in areas where forests were not subjected to conversion (Caquet et al. 2010). Strong (2011) looked at the laterally cast shadows of western white spruce to determine if shadowing affected understory growth in boreal forest stands with a quaking

aspen canopy. Results presented by Strong (2011) indicated that canopy cover had less of an effect on understory growth than western white spruce shadows. A unique approach, examination of shadow casting may be used to explain unusual understory

effects within primary and secondary successional species and would be a new element for use in predicting climate change responses.

Table 3. Sample site coordinates and biome designations

Sample Sites	Designation	Site Name	Latitude	Longitude	Biome Designation
Oregon	AND	HJ Andrews Experimental Forest	44.21	-122.26	Temperate Deciduous Forest
Alaska	ARC	Arctic Basin	68.63	-149.60	Tundra/Taiga
Arizona	CAP	Central Arizona–Phoenix	33.43	-111.93	Desert
Canada	CAS	Casper Creek Experimental Watershed	50.22	122.22	Boreal
North Carolina	CWT	Coweeta Hydrologic Laboratory	35.00	-83.50	Temperate Deciduous Forest
Florida	FCE	Florida Coastal Everglades	25.47	-80.85	Tropical Deciduous Forest
West Virginia	FER	Fernow Experimental Forest	39.03	79.41	Coniferous Forest
Colorado	FRA	Fraser Experimental Forest	39.85	105.91	Coniferous Forest
Michigan	KBS	Kellogg Biological Station	42.40	-85.40	Tallgrass prairie
Kansas	KNZ	Konza Prairie	39.10	-96.40	Prairie / Grassland
Puerto Rico	LUQ	Luquillo Experimental Forest	18.30	-65.80	Tropical Deciduous Forest
Wisconsin	NTL	North Temperate Lakes	46.00	-89.70	Temperate Forest Biome
Colorado	NWT	Niwot Ridge	39.99	-105.38	Tundra/Taiga
California	SGS	Shortgrass Steppe	40.80	-104.80	Grassland / Steppe
Montana	TEN	Tenderfoot Creek Experimental Forest	46.55	110.53	Coniferous Forest

Table 4. Total yearly precipitation across the various biome sites¹

Year	AND	ARC	CAP	CAS	CWT	FCE	FER	FRA	KBS	KNZ	LUQ	NTL	NWT	SGS	TEN
1990	2152.9	230	253	1050.5	2094.5	1158	1590	550.9	1019.9	570.3		928.9	1827	356.9	
1991	2035.3	321.6	262	897.8	1732	1436.4	1323.8	583.9	978	569.7		994.2	1908	351	
1992	1840.8	374	502	1296.4	2281.4	1290.8	1337.3	537	843.5	885.9		817.3	1538	359	
1993	1888.7	243.5	401	1264.6	1584.5	1317.2	1446.7	663.7	806.7	1227.6	2673.4	1102.3	2026	390.7	195.1
1994	2004.8	277.1	341	888.2	2134.9	1373.7	1772.1	481.8	918.5	635.6	1634.9	853.2	1631	255.9	676.2
1995	2624.3	317.4	340	1699.4	1930.4	1933.2	1334	793.8	762.9	942.1	2337.6	854.1	2698	432.6	978.3
1996	3379.4	342.9	238	1632.4	2040.6	1072.1	2051	704.3	693.6	683.6	3970.6	805.6	2834	390.9	879.1
1997	2089	428	131	1200.8	1948.5	1253.5	1582.4	635.3	775.5	628.1	3505.3	731.9	2446	557.3	855.9
1998	2568	266.4	236	1995.8	1743.4	1467.6	1448	553.5	722.7	944	7770.9	1015.4	1795	330.8	830.9
1999	2470.2	361.9	173	1284.7	1572	1475.1	1300	595.1	608.2	825.2	5368.4	812.2	2631	513.1	757.3
2000	1922.7	330.6	258	1062.9	1234.4	896.5	1307.9	689.4	937.6	626.6	1029	1023.8	2574	228.5	714.3
2001	1844.2	247.8	142	1350.7	1394.9	1495.7	1400.3	493.5	1033	892.1	2910.2	978.1	2187	293.1	677.4
2002	1773.1	386.4	214.1	1208.9	1783.6	1321.9	1565.6		731.5	656.2	1488.1	665.9	1795	185.2	727.1
2003	2332.8	462.5	201.7	1358.4	2108.5	1607.8	1652.5		908.9	722.6	4012.7	806.8	2403	300.4	815.9
2004	1873.7	263.7	122.9	1039	1825	313.1	1735.8		959.4	990.4	3474.2	1001.6	2194	278.3	43.1
2005	2027.2	215.6		903.7	2058.4	437.1	1392.9		700.3	951.9	3513.4	628.6	2377	385.9	
2006	2471.2	376.2			1549.6	767.1	1501.3		1150	660.6		933.4	2259	264.6	
2007	241.8				1212.9	388.6			495.8			1026.4		287.1	
2008															

¹Precipitation data in millimeters (mm). Raw data can be found at <http://www.iternet.edu/>

AND: HJ Andrews Experimental Forest; ARC: Arctic Basin; CAP: Central Arizona–Phoenix; CAS: Casper Creek Experimental Watershed; CWT: Coweeta Hydrologic Laboratory; FCE: Florida Coastal Everglades; FER: Fernow Experimental Forest; FRA: Fraser Experimental Forest; KBS: Kellogg Biological Station; KNZ: Konza Prairie; LUQ: Luquillo Experimental Forest; NTL: North Temperate Lakes; NWT: Niwot Ridge; SGS: Shortgrass Steppe; TEN: Tenderfoot Creek Experimental Forest

Conclusions

These data make it clear that future climate shifts have the potential to forever alter the species composition of forests around the world. This synthesis of data showed that inclusion of drought

tolerance and shade tolerance with respect to size-density relationships needs additional exploration. Although shade and drought tolerance have been well studied by a number of research groups, this review reveals that in-depth analysis of a single or a few species in a given area will not generate the data required to implement a successful regeneration plan. Use of data

acquired from a large variety of species using the same or highly similar models and additional physiological variables within a wide range of theoretical climates would be an exceedingly beneficial study or collection of studies as data obtained from modeling is highly dependent upon the model and parameters manipulated.

Furthermore, to improve the diversity of tree species within our forests and to ensure that endangered species are not further decimated by inability to survive in a given climate, strategies involving additional successional stages to thoroughly address this problem and others such as forest responses to disease and pests are needed. A greater understanding of how spatial patterns of harvest interact with tree removal intensity to affect understory light conditions can provide opportunities for designing silvicultural prescriptions that are tailored to species' traits and better suited to meet a variety of management objectives. Thus, in order to develop the best management plans, future experiments should be focused on broader evaluations of modeling data to ensure its suitability for predicting forest cover in a particular area. This review highlights the need for studies on a wider range of species using historical accounts of previous species composition, information regarding site seasonality, species competition, and individual responses to altered light conditions. Also, use of more innovative methods to evaluate the effects of altered light, temperature, and precipitation regimes on species diversity such as use of shadow casting data should be considered to help understand and perhaps minimize negative effects of environmental changes on the world's forests.

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Appendix 1. Estimated drought and shade tolerances for the tree and shrub species mentioned within the review.

Genus	Scientific Name	Shade Tolerance*	Drought Tolerance*	References
		low → high	low → high	
<i>Abies</i>	<i>A. alba</i>	moderate → high	low	Nagel et al. 2010; Vielliedent et al. 2010; Pantic et al. 2011; Ameztegui et al. 2012
	<i>A. alba</i> 'Pendula'	low → moderate	low	Vielliedent et al. 2010
	<i>A. balsamea</i>	low → high	low	Boivin et al. 2010
	<i>A. concolor</i> 'lowiana'	moderate	moderate → high	Hawkins et al. 2011
	<i>A. lasiocarpa</i>	highly tolerant	low	Antos et al. 2010
<i>Acacia</i>	<i>A. auriculiformis</i>	low/intolerant	moderate → high	Wang et al. 2013
	<i>A. koa</i>	low/intolerant	moderate → high	Scowcroft and Yeh 2013
	<i>A. mangium</i>	low/intolerant	low/intolerant	Craven et al. 2011; Wang et al. 2013
<i>Acer</i>	<i>A. campestre</i>	low → moderate	moderate → high	Caquet et al. 2010
	<i>A. negundo</i>	low/intolerant	low/intolerant	Saccone et al. 2010
	<i>A. pictum</i> 'Mono'	low → moderate	low → high	Takahashi 2010
	<i>A. platanoides</i>	low/intolerant	moderate → high	Caquet et al. 2010; Martin et al. 2010
	<i>A. pseudoplatanus</i>	low/intolerant	moderate	Morecroft et al. 2008; Caquet et al. 2010; Mund et al. 2010; Nagel et al. 2010; Le Gof et al. 2011
	<i>A. saccharum</i>	highly tolerant	moderate → high	Auclair et al. 2010; Cowell et al. 2010; Dyer et al. 2010; Gasser et al. 2011
<i>Agrostis</i>	<i>A. gigantea</i>	low → moderate	moderate	Dey et al. 2010
<i>Ailanthus</i>	<i>A. altissima</i>	low/intolerant	moderate → high	Martin et al. 2010
<i>Alstonia</i>	<i>A. macrophylla</i>	low → high	low → high	Goodale et al. 2012
<i>Austrocedrus</i>	<i>A. chilensis</i>	moderate	moderate → high	Gyenge et al. 2003; Gyenge et al. 2008b
<i>Beilschmiedia</i>	<i>B. tawa</i>	low → moderate	low	Carswell et al. 2012
<i>Betula</i>	<i>Betula</i> spp.	low → moderate	low	Auclair et al. 2010; Tanentzap et al. 2013
	<i>B. alleghaniensis</i>	moderate	low	Gasser et al. 2010
	<i>B. maximowicziana</i>	intolerant	low → moderate	Takahashi 2010
	<i>B. papyrifera</i>	intolerant	low → moderate	Luo et al. 2011
<i>Biota</i>	<i>B. orientalis</i>	low → moderate	low	Khamzina et al. 2006
<i>Camellia</i>	<i>C. tsaii</i>	low → moderate	low/intolerant	Van Do et al. 2011
<i>Caragana</i>	<i>C. korshinskii</i>	low/intolerant	moderate	Guo and Shao 2013

Continue Appendix 1

Genus	Scientific Name	Shade Tolerance*	Drought Tolerance*	References
		low → high	low → high	
<i>Carya</i>	<i>C. cordiformis</i>	moderate → high	low	Dyer et al. 2010
	<i>C. illinoensis</i>	low/intolerant	high	Jacobs et al. 2012; Steele et al. 2013
	<i>C. ovata</i>	low/intolerant	low	Karnitz and Asbjornsen 2006; Sauer et al. 2012
<i>Castanea</i>	<i>C. sativa</i>	moderate	moderate → high	Álvarez-Álvarez et al. 2013
	<i>C. coudereii</i>	low → moderate	low → moderate	Álvarez-Álvarez et al. 2013
<i>Castanopsis</i>	<i>C. fissa</i>	moderate	moderate → high	Wang et al. 2013
	<i>C. hystrix</i>	moderate	moderate → high	Wang et al. 2013
<i>Cercis</i>	<i>C. canadensis</i>	low → moderate	low → moderate	Hartman and McCarthy 2004
<i>Colubrina</i>	<i>C. glandulosa</i>	low → moderate	low	Craven et al. 2011
<i>Cornus</i>	<i>C. florida</i>			Hartman and McCarthy 2004
<i>Dacrydium</i>	<i>D. cupressinum</i>	moderate	low	Carswell et al. 2012
<i>Dillenia</i>	<i>D. triquetra</i>	moderate → high	moderate	Goodale et al. 2012
<i>Dipterocarpus</i>	<i>D. sublamellatus</i>	low → high	low → moderate	Kosugi et al. 2009; Makita et al. 2012
<i>Elaeagnus</i>	<i>E. angustifolia</i>	low/intolerant	moderate → high	Khamzina et al. 2006; Reynolds and Cooper 2010
<i>Eucalyptus</i>	<i>Eucalyptus</i> spp.	low → moderate	low → high	Brockerhoff et al. 2013
	<i>E. urophylla</i>	low/intolerant	low → moderate	Wang et al. 2013
	<i>E. tereticornis</i>	low/intolerant	low → moderate	Wang et al. 2013
<i>Fagus</i>	<i>F. grandifolia</i>	low → moderate	low	Cowell et al. 2010; Siegert and Levia 2011
	<i>F. orientalis</i>	low → high	moderate → high	Akhaven et al. 2012
	<i>F. sylvatica</i>	low → high	low → high	Caquet et al. 2010; Mund et al. 2010; Nagel et al. 2010; Jarcuska and Barna 2011b; Le Goff et al. 2011; Petritan et al. 2011; Rivoire and Le Moguegec 2012
<i>Fraxinus</i>	<i>Fraxinus</i> spp.	low → moderate	low → moderate	Karnitz and Asbjornsen 2006
	<i>F. americana</i>	moderate	low	Auclair et al. 2010; Dyer et al. 2010
	<i>F. excelsior</i>	high	high	Morecroft et al. 2008; Maltoni et al. 2010 Mund et al. 2010; Le Goff et al. 2011
	<i>F. nigra</i>	moderate	low → moderate	Livingston et al. 1995; Auclair et al. 2010
	<i>F. ornus</i>	low/intolerant	low	Csontos et al. 2001
	<i>F. pennsylvanica</i>	moderate	moderate	Hartman and McCarthy 2004; Karnitz and Asbjornsen 2006; Andrews et al. 2010; Auclair et al. 2010; Jacobs et al. 2012
<i>Inga</i>	<i>I. punctata</i>	low/intolerant	moderate → high	Craven et al. 2011
<i>Juglans</i>	<i>J. nigra</i>	low/intolerant	low	Hartman and McCarthy 2004; Sauer et al. 2012; Steele et al. 2013
<i>Larix</i>	<i>L. occidentalis</i>	low/intolerant	moderate → high	Newsome et al. 2010; Leites et al. 2012
<i>Leguminosae</i>	<i>Leguminosae</i> spp.	low → high	low → high	Makita et al. 2012
<i>Ligustrum</i>	<i>L. japonicum</i>	low/intolerant	low	Yoko-o et al. 2011
<i>Liquidambar</i>	<i>L. styraciflua</i>	low/intolerant	low	Hanberry et al. 2012
	<i>L. formosana</i>	low/intolerant	moderate	Wei et al. 2013
<i>Liriodendron</i>	<i>L. tulipifera</i>	low/intolerant	low	Morrissey et al. 2008; Siegert and Levia 2011
<i>Lithocarpus</i>	<i>L. ducampii</i>	moderate → high	moderate → high	Tran Van Do et al. 2011
<i>Macaranga</i>	<i>M. indica</i>	low/intolerant	low	Goodale et al. 2012
	<i>M. peltata</i>	low/intolerant	low	Goodale et al. 2012
<i>Melastoma</i>	<i>M. malabathricum</i>	low → moderate	low/intolerant	Goodale et al. 2012
<i>Michelia</i>	<i>M. macclurei</i>	low → moderate	low/intolerant	Wang et al. 2013
<i>Morus</i>	<i>M. alba</i>	moderate → high	moderate → high	Khamzina et al. 2006
<i>Neolitsea</i>	<i>N. aciculata</i>	moderate → high	moderate → high	Nanami et al. 2011
<i>Northofagus</i>	<i>N. betuloides</i>	low/intolerant	low → moderate	Promis et al. 2010
	<i>N. nitida</i>	low/intolerant	low	Coopman et al. 2011
	<i>N. fusca</i>	intolerant	moderate	Hurst et al. 2012
	<i>N. menziesii</i>	intolerant	low/intolerant	Hurst et al. 2012
	<i>N. pumilio</i>	intolerant/low	low	Promis et al. 2010b
<i>Ostrya</i>	<i>O. virginiana</i>	low → moderate	moderate	Karnitz and Asbjornsen 2006; Dyer et al. 2010; Matonis et al. 2011
<i>Picea</i>	<i>P. abies</i>	low/intolerant	low	Vieilledent et al. 2010; Petritan et al. 2011; Rivoire and Le Moguegec 2012
	<i>P. engelmannii</i>	low → moderate	low	Antos et al. 2010
	<i>P. glauca</i>	low → moderate	high	Kabzems et al. 2011; Strong 2011; Thiffault et al. 2013
	<i>P. mariana</i>	low/intolerant	low → moderate	Luo et al. 2011; Coursolle et al. 2012; Tremblay et al. 2013; Thiffault et al. 2013
	<i>P. rubens</i>	moderate → high	moderate	Auclair et al. 2010
	<i>P. sitchensis</i>	low/intolerant	low	Pabst and Spies 1999; Comeau et al. 2010; Sarr et al. 2011

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Genus	Scientific Name	Shade Tolerance*	Drought Tolerance*	References
		low → high	low → high	
<i>Pinus</i>	<i>Pinus</i> spp.	low → moderate	low → high	Poulos et al. 2012
	<i>P. attenuata</i>	low/intolerant	high	Poulos et al. 2012
	<i>P. banksiana</i>	low/intolerant	moderate → high	Luo et al. 2011; Coursolle et al. 2012
	<i>P. contorta</i>	low/intolerant	low	Poulos et al. 2012
	<i>P. coulteri</i>	low/intolerant	moderate → high	Poulos et al. 2012
	<i>P. elliotii</i>	low → moderate	moderate	Wei et al. 2013
	<i>P. halipensis</i>	low/intolerant	moderate → high	Maestre et al. 2003; Maestre and Cortina 2004; Querejeta et al. 2008; Puertolas et al. 2010; Prevosto et al. 2011; Navarro et al. 2013
	<i>P. lamertiana</i>	moderate	low	Poulos et al. 2012
	<i>P. massoniana</i>	low/intolerant	moderate	Wei et al. 2013
	<i>P. mugo</i>	low/intolerant	moderate → high	Ameztegui et al. 2012
	<i>P. nigra</i>	low/intolerant	moderate → high	Lucas-Borja et al. 2011; Mataruga et al. 2012
	<i>P. ponderosa</i>			Gyenge et al. 2003; Gyenge et al. 2008b
	<i>P. radiata</i>	moderate	moderate → high	Meers et al. 2010
	<i>P. strobus</i>	moderate	low	Coursolle et al. 2012; Sauer et al. 2012
	<i>P. sylvestris</i>	low/intolerant	moderate	Gaudio et al. 2011; Ameztegui et al. 2012; Sauer et al. 2012
	<i>P. uncinata</i>	low/intolerant	moderate → high	Ameztegui et al. 2012
<i>Pittosporum</i>	<i>P. tobira</i>	low/intolerant	moderate → high	Yoko-o et al. 2011
<i>Platanus</i>	<i>P. occidentalis</i>	low/intolerant	moderate	Andrews et al. 2010; Steele et al. 2013
<i>Podocarpus</i>	<i>P. nagi</i>	low/intolerant	moderate → high	Nanami et al. 2011
<i>Populus</i>	<i>P. deltoides</i>	low/intolerant	moderate → high	Steele et al. 2013
	<i>P. euphratica</i>	low/intolerant	moderate	Khamzina et al. 2006
	<i>P. nigra</i>	moderate	low	Reynolds and Cooper 2010
	<i>P. maximowiczii</i>	intolerant	low → moderate	Takahashi 2010
	<i>P. tremuloides</i>	low → moderate	low	Boivin et al. 2010; Kabzems et al. 2011; Luo et al. 2011; Strong 2011; Coursolle et al. 2012
<i>Prumnopitys</i>	<i>P. ferruginea</i>	low → moderate	low	Carswell et al. 2012
<i>Prunus</i>	<i>P. armeniaca</i>	moderate → high	moderate	
	<i>P. emarginata</i>	moderate → high	moderate → high	Brown and Antos 2012
	<i>P. serotina</i>	low/intolerant	high	Hartman and McCarthy 2004; Siegert et al. 2011; Siegert and Levia 2011
<i>Pseudotsuga</i>	<i>P. guachapele</i>	low/intolerant	moderate → high	Craven et al. 2011
<i>Pseudotsuga dosamanea</i>				
<i>Pseudotsuga</i>	<i>P. menziesii</i> ‘Menziesii’	low/intolerant	moderate → high	Wharton et al. 2009; Comeau et al. 2010; Newsome et al. 2010; Rathbun et al. 2010; Petritan et al. 2011; Brown and Antos 2012; Coursolle et al. 2012
<i>Quercus</i>	<i>Quercus</i> spp.	low → moderate	low → high	Steele et al. 2013
	<i>Q. alba</i>	moderate	low	Rebbeck et al. 2012
	<i>Q. canariensis</i>	low → moderate	moderate → high	Gómez-Aparicio et al. 2008
	<i>Q. frainetto</i>	low → moderate	moderate → high	Vlachodimos et al. 2013
	<i>Q. glauca</i>	low/intolerant	low	Yoko-o et al. 2011
	<i>Q. ilex</i>	low → moderate	moderate → high	Gómez-Aparicio et al. 2008; Puertolas et al. 2010; Rodríguez-Calcerrada et al. 2011
	<i>Q. muehlenbergii</i>	low/intolerant	moderate → high	Hartman and McCarthy 2004
	<i>Q. nigra</i>	moderate	low	Jacobs et al. 2012
	<i>Q. nuttallii</i>	low/intolerant	moderate	Jacobs et al. 2012
	<i>Q. pagoda</i>	low/intolerant	low	Jacobs et al. 2012
	<i>Q. plaustris</i>	low/intolerant	moderate	Andrews et al. 2010
	<i>Q. patraea</i> ‘Sessiliflora’	low → moderate	low → moderate	Rodríguez-Calcerrada et al. 2010; Gaudio et al. 2011; Le Goff et al. 2011; Rivoire and Le Moguegec 2012
	<i>Q. prinus</i>	low/intolerant	low	Rebbeck et al. 2012
	<i>Q. pyrenaica</i>	moderate	low	Gómez-Aparicio et al. 2008; Rodríguez-Calcerrada et al. 2010
	<i>Q. robur</i>	low/intolerant	moderate → high	Morecroft et al. 2008; Rivoire and Le Moguegec 2012
	<i>Q. rubra</i>	moderate	moderate	Casperson and Kobe 2001; Rebbeck et al. 2012; Sauer et al. 2012
	<i>Q. suber</i>	low → moderate	moderate → high	Gómez-Aparicio et al. 2008; Mecherghi et al. 2013
<i>Robinia</i>	<i>R. pseudoacacia</i>	low/intolerant	low → moderate	Athy and Keiffer 2003; Vlachdimos et al. 2013
<i>Salix</i>	<i>S. nigra</i>	low/intolerant	low/intolerant	Khamzina et al. 2006
	<i>S. purpurea</i>	low → moderate	moderate	Ens et al. 2013
	<i>Salix</i> spp.	low/intolerant	low	Linderson et al. 2007; Saccone et al. 2010; Savage et al. 2012; Savage and Cavendar-Bares 2012

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Genus	Scientific Name	Shade Tolerance*	Drought Tolerance*	References
		low → high	low → high	
<i>Schima</i>	<i>S. superba</i>	low/intolerant	low → moderate	Wang et al. 2013; Wei et al. 2013
	<i>S. wallichii</i>	low → moderate	low → moderate	Van Do et al. 2011
<i>Schumacheria</i>	<i>C. castaneifolia</i>	moderate → high	moderate	Goodale et al. 2012
<i>Shorea</i>	<i>Shorea</i> spp.	low → high	low → high	Makita et al. 2012
<i>Sorbus</i>	<i>S. aucuparia</i>	low/intolerant	low	Zyweic and Holeksa 2012
<i>Tamarix</i>	<i>T. ramosissima</i>	low/intolerant	moderate → high	Reynolds and Cooper 2010
	<i>T. androssowii</i>	low/intolerant	moderate → high	Khamzina et al. 2006
<i>Taxus</i>	<i>T. baccata</i>	low → high	low → high	Iszkulo 2010
<i>Tectona</i>	<i>T. grandis</i>	low/intolerant	moderate → high	Craven et al. 2011
<i>Terminalia</i>	<i>T. amazonia</i>	low/intolerant	moderate	Craven et al. 2011
<i>Thuja</i>	<i>T. plicata</i>	moderate → high	low	Newsome et al. 2010; Rathbun et al. 2010
<i>Thujopsis</i>	<i>T. dolabrata</i>	low/intolerant	low	Hitsuma et al. 2012
<i>Tilia</i>	<i>T. americana</i>	low/intolerant	low	Cowell et al. 2010; Dyer et al. 2010
	<i>T. japonica</i>	low → moderate	low → high	Takahashi 2010
<i>Trema</i>	<i>T. orientalis</i>	low/intolerant	high	Goodale et al. 2012
<i>Tsuga</i>	<i>T. chinensis</i>	low → high	low	Pabst and Spies 1999; Rathbun et al. 2010; Sarr et al. 2011
	<i>T. heterophylla</i>	high	low	Reynolds and Cooper 2010
<i>Ulmus</i>	<i>U. americana</i>	low/intolerant	moderate → high	Karnitz and Asbjornsen 2006; Cowell et al. 2010
	<i>U. pumila</i>	low/intolerant	moderate → high	Khamzina et al. 2006
<i>Wendlandia</i>	<i>W. bicuspidata</i>	moderate → high	moderate	Goodale et al. 2012
	<i>W. peniculata</i>	moderate → high	moderate	Van Do et al. 2011

*When the referenced article did not mention a specific drought or shade tolerance the online resources <http://www.pfaf.org/user/plantsearch.aspx>, http://www.na.fs.fed.us/spfo/pubs/silvics_manual/table_of_contents.htm, and http://hort.ufl.edu/database/documents/pdf/tree_fact_sheets/picglaa.pdf were used for clarification. Tolerance levels with a range arrow (→) indicate a range of tolerances reported in the literature.